



Biochemical systematics of the Wood mouse, *Sylvaemus sylvaticus* (L., 1758) sensu lato (Rodentia, Muridae) from eastern Europe and Asia

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Abstract

A reexamination of species identity of oriental subspecies of *Sylvaemus sylvaticus* are performed on the basis of allozyme data. Practically all oriental *S. sylvaticus* subspecies (*charkovensis*, *baessleri*, *mosquensis*, *ciscaucasicus*, *uralensis*, *tsherga*, *pallipes*) have been identified as *S. microps s.l.* Only *S. s. vohlynsensis* is identical to nominative *S. sylvaticus*. The most eastern forms of wood mouse, *kastschenkoi*, from the Altai mountains, and, *pallipes*, from Tadjikistan, can be characterized by fixed allelic variants at a few loci distinguishable both from nominative *S. microps* and one another at the allo-species level. Taxonomic analysis confirms that the name *uralensis* Pallas, 1811, is the oldest available name for a group of *S. microps*-like forms.

Introduction

Despite large interest in the wood mice genus *Sylvaemus* Ognev, 1924, the systematic problems of this taxonomic group have not solved. This may be due to both wide geographic and individual variability throughout the area and by chromosome formula stability. Only in the last decade after implication of biochemical genetic data, has the wood mice genus *Apodemus s.l.* been revised. The main results were: (i) the genera distinctness of eastern (*Apodemus* and *Alsomys*) and western (*Sylvaemus* and *Karstomys*) Palearctic subgenera (GEMMEKE 1980; ISKANDAR and BONHOMME 1984; BRITTON-DAVIDIAN et al. 1991; MEZH ZHERIN and ZYKOV 1991; FILIPPUCI 1993); (ii) species level differentiation of the following taxa: *S. alpicola* (Heinrich, 1952) (STORCH and LÜTT 1989; VOGEL et al. 1992), *S. fulvipectus* Ognev, 1924 (= *falzfeini* Mezhzherin and Zagorodnyuk, 1989) (MEZH ZHERIN and ZAGORODNYUK 1989; VORONTZOV et al. 1992), *S. hermonensis* (Filippucci, Simson et Nevo, 1989) (FILIPPUCI et al. 1989), *S. hyrkanicus* (VORONTZOV, BOESKOROV, MEZH ZHERIN, 1992) (VORONTZOV et al. 1992), *S. ponticus* (Sviridenko, 1936) (MEZH ZHERIN 1991; VORONTZOV et al. 1992).

The wood mouse *S. sylvaticus* (L., 1758) is one of the widest geographically distributed species of Palearctic muroid rodents. Its range extends from central Asian mountains and the Altai on the east, to northern Africa and the British Isles on the west. Biochemical variation analysis of *Sylvaemus sylvaticus* s. lato populations of eastern Europe and Asia have detected that several subspecies of *S. sylvaticus* (*S. s. uralensis*, *S. s. charkovensis*, *S. s. tsherga*, *S. s. mosquensis* and *S. s. ciscaucasicus*) were found to be geographic forms of *S. microps* (MEZH ZHERIN 1987, 1990; MEZH ZHERIN and ZYKOV 1991; MEZH ZHERIN and MIKHAILENKO 1991; MEZH ZHERIN et al. 1992; VORONTZOV et al. 1992).

Nevertheless, these results require generalization. Therefore, the main task of the investigation consisted in summarizing of biochemical variation and differentiation data of wood mice, *S. sylvaticus*, geographic forms from the former USSR territory.

Material and methods

Electrophoretic analysis was carried out on 293 specimens representing populations of *S. s. sylvaticus* live-trapped throughout the former USSR territory in Armenia, Belorussia, Russia, Ukraine, and Tadjikistan. A list of investigated subspecies, their collecting sites, and the number of specimens examined for each taxon are presented in table 1. Sample localities are illustrated in figure 1.

Each specimen was tested in the laboratory for plasma and hemolysed red cells, and tissue samples (liver, kidney, muscle) were immediately studied by standard vertical 7.5% acrylamide gel electrophoresis. Muscle, kidney and liver were homogenized in distilled water containing 5% sucrose and tested for the enzymes and proteins listed in table 2.

Loci were designated according to nomenclature adapted for laboratory mice strains (BONHOMME et al 1984). Allozymes were designated numerically according to their mobility, relative to the most common allele (= 100) in *S. s. sylvaticus* specimens (< 100 = slower mobility; > = faster mobility). In present study included loci of nonspecific esterases having a reliable homology in *S. microps* and *S. sylvaticus* by electrophoretic interspecies comparison.

The genetic divergence between taxa was estimated with the indices of standard (NEI 1975) and unbiased (NEI 1978) genetic distances. A dendrogram of genetic relationship among populations was obtained by using an UPGMA algorithm.

Table 1. Number of specimens examined by electrophoretic procedures for each subspecies and locality

N	Taxa	Localities	n	
1	<i>S. s. sylvaticus</i>	Slovakia	Komarno	3
		Ukraine	Cherkassy region	7
			Nikolaev region	26
			Odessa region	5
			Kishinev	8
2	<i>S. s. vohlynenis</i>	Ukraine	Kiev region	23
		Belorussia	Gomel region	14
3	<i>S. s. charkovensis</i>	Ukraine	Charkov region	6
			Lugansk region	12
			Cherson region	30
4	<i>S. s. baessleri</i>	Ukraine	Crimea	6
5	<i>S. s. mosquensis</i>	Russia	Moskow region	12
6	<i>S. s. ciscaucasicus</i>	Russia	Kabardino-Balkaria	14
			Northern Osetia	7
			Krasnodar region	4
		Armenija	Khosrov reserve	5
			Russia	Saratov region
7	<i>S. s. uralensis</i>	Russia	Uralsk region	8
			Kurgan region	6
			Chelabinsk region	3
			Altai	37
8	<i>S. s. kastschenkoi</i>	Russia	Altai	37
9	<i>S. s. pallipes</i>	Tadjikistan	Komsomolabad district	9
10	<i>S. microps</i>	Slovakia	Komarno	5
		Moldova	Kishinev region	36
		Ukraine	Nikolaev region	4

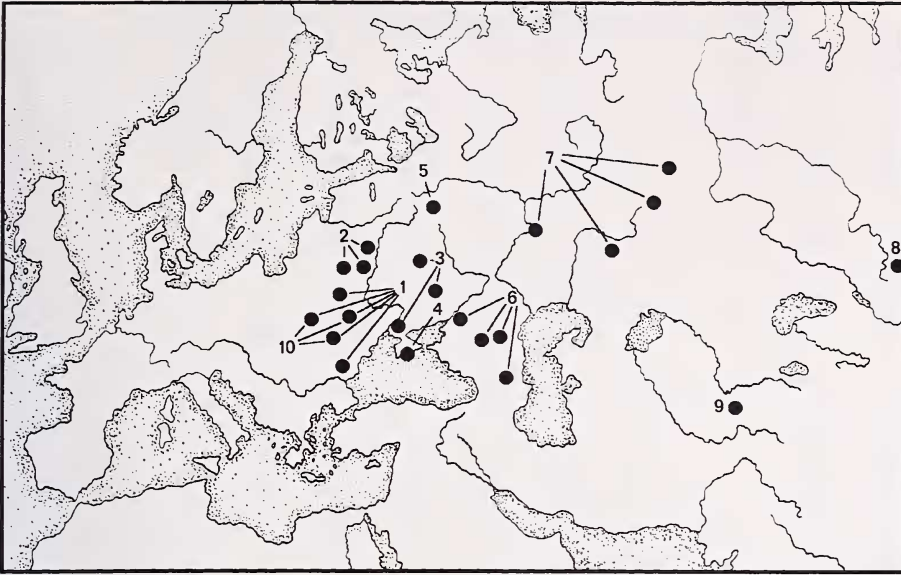


Fig. 1. Sample localisations of *S. sylvaticus* taxa and *S. microps* populations used in genetic investigations.

Table 2. Buffer systems, loci scored and tissue expression in the analysis of *S. sylvaticus* s. l.

Enzyme or protein	E.C. number	Locus	Tissue	Buffer system
Albumin		Alb	l, m, pl	B
Alcohol dehydrogenase	1.1.1.1	Adh-1	l	A
Aspartate aminotransferase	2.6.1.1	Aat-1, 2	m, k, l	A
Carbonic anhydrase	4.2.1.1	Car-1	hem	A, B
Creatine kinase	2.7.3.2	Ck-2	m	A, B
Diaphorase	1.6.2.2	Dia-1, 2	h	A, B
Esterase	3.1.1.1	Es-1, 2, a	pl	B
		Es-9, 15	m	A, B
		Es-3, 6, 10	k	A, B
Glucose-6-phosphate dehydrogenase	1.1.1.49	Gpd-x	k, l	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	Gdc-1	k, m	A
Hemoglobin		Hb-A, B	hem	A, B
Isocitrate dehydrogenase	1.1.1.42	Idh-1	l, k	A
		Idh-2	m	A
Lactate dehydrogenase	1.1.1.27	Ldh-A	m, k, l	A
		Ldh-B	k, m	A
Malate dehydrogenase	1.1.1.37	Mor-1, 2	m, k, l	A
Malic enzyme	1.1.1.40	Mod-1, 2	m, k, l	A
Phosphoglucomutase	2.7.5.1	Pgm-1	m	B
		Pgm-2	m, k, l	B
Phosphogluconate dehydrogenase	1.1.1.44	Pgd	m, k, l	A
Postalbumin		Post	pl	B
Superoxide dismutase	1.15.1.1	Sod-1	m, l	A
		Sod-2	m	B
Sorbitol dehydrogenase	1.1.1.14	Sdh	l, k	A
Transferrin		Tf	p	B
Xanthine dehydrogenase	1.2.3.2	Xdh	l	A

Buffer type abbreviations are as follows: A – continuous Tris-EDTA-borate (pH 8.5) (PEACOCK et al. 1965), B – discontinuous Tris-glycine (pH 8.3) and Tris-HCl (pH 8.7) (DAVIS 1964). k – kidney, l – liver, m – muscle, hem – hemolysate, pl – plasma.

Table 3. (Continued)

Loci	Alleles	1	2	3	4	5	6	7	8	9	10
		<i>S. s.</i> <i>sylv.</i>	<i>S. s.</i> <i>vohl.</i>	<i>S. s.</i> <i>char.</i>	<i>S. s.</i> <i>baes.</i>	<i>S. s.</i> <i>mos.</i>	<i>S. s.</i> <i>cis.</i>	<i>S. s.</i> <i>ural.</i>	<i>S. s.</i> <i>tscher.</i>	<i>S. s.</i> <i>pall.</i>	<i>S.</i> <i>micr.</i>
Pgd	100	1.00	1.00	0.96	0.50	0.76	0.73	0.75	1.00	1.00	1.00
	104			0.04	0.50						
	105					0.24	0.27	0.25			
Post	100	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00
	110						0.10				
Sod-1	100			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	110	1.00	1.00								
Tf	90	0.88	0.84								
	92			0.02		0.07		0.07			
	95	0.07	0.16								
	97.5									0.61	
	98			0.28	0.60	0.32	0.50	0.49	1.00		0.65
	99.5									0.39	
	100			0.65	0.40	0.50	0.46	0.42			0.31
	101	0.05									
	102			0.05		0.11	0.04				0.04
Xdh	97			0.17		0.08	0.15		0.37		0.07
	100	0.81	0.75	0.83	1.00	0.92	0.85	1.00	0.63	1.00	0.93
	102	0.19	0.25								
n	59	37	48	6	12	30	19	37	9	45	
H obs, %		4.56	4.08	4.08	4.66	4.11	6.00	6.19	1.83	3.77	4.42
H exp, %		4.89	5.33	4.17	4.67	4.14	6.25	7.19	1.86	3.78	4.17
A		1.19	1.14	1.25	1.14	1.17	1.25	1.28	1.06	1.14	1.14
P, 1%		13.9	11.1	19.4	13.9	11.1	30.5	19.4	5.6	13.9	11.1

1 – *S. s. sylvaticus*, 2 – *S. s. vohlynenis*, 3 – *S. s. charkovensis*, 4 – *S. s. baessleri*, 5 – *S. s. mosquensis*,

6 – *S. s. ciscaucasicus*, 7 – *S. s. uralensis*, 8 – *S. s. kastschenkoi*, 9 – *S. s. pallipes*, 10 – *S. s. microps*.

Results

Biochemical variation.

Sixteen out of 36 loci analysed were monomorphic and fixed for the same allele in all populations studied; Adh-1, Aat-1, Ck-2, Dia-1,2, Es-6, Gpd-X, Mor-1,2, Mod-2, Pgm-1,2, Sdh, Sod-2, Hb-A, Alb. The allele frequencies of variable loci in the taxa analysed are given in table 3.

Levels of genetic variation are given in table 3: mean number of alleles per locus (A); mean proportion of heterozygosity observed (Hobs) and expected (Hexp); proportion of polymorphic loci per population (P, I%).

A high level of polymorphism was found at the following loci: Gdc-1, Idh-1, Tf, Es-1,2, Pgdh, Xdh, in at least one subspecies or population. Eight loci: Aat-2, Car-1, Es-9,15, Idh-2, Ldh-A,B, Post had only rare allelic variants. Average estimation of intrapopulation genetic variation (Tab. 3) was higher than usually observed in mammals (NEVO et al. 1984; MEZHNERIN 1992); range was from H obs = 0.018 to 0.062 with mean H obs = 0.044. The highest levels H obs = 0.06 and 0.062 were found in *S. s. uralensis* and *S. s. ciscaucasicus*, respectively, whereas the lowest ones were revealed in Altay subspecies H obs = 0.018.

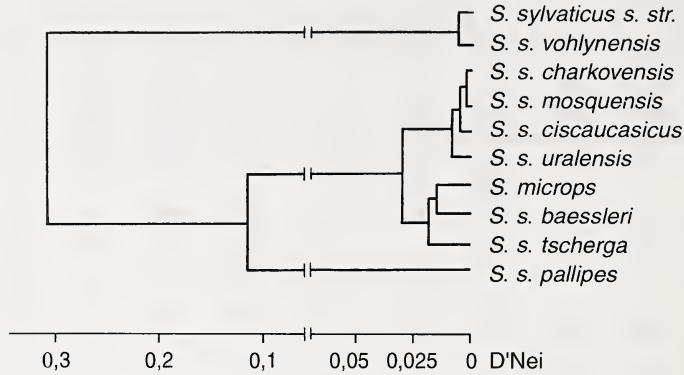


Fig. 2. UPGMA phenogram of genetic distances (Nei 1975) between *S. sylvaticus* taxa and *S. microps* based on 36 biochemical loci.

Table 4. Matrix of standard Nei's (1975) genetic distances (below diagonal) and unbiased Nei's (1978) genetic distance (above diagonal) among *S. sylvaticus* s.l. subspecies

Taxa	N	1	2	3	4	5	6	7	8	9	10
<i>S. sylvaticus</i> s. str	1	0	0.003	0.251	0.252	0.258	0.254	0.257	0.258	0.248	0.244
<i>S. s. vohlynensis</i>	2	0.004	0	0.250	0.244	0.268	0.269	0.262	0.248	0.258	0.238
<i>S. s. charkovensisa</i>	3	0.312	0.309	0	0.018	0.001	0.004	0.011	0.028	0.092	0.011
<i>S. s. baessleri</i>	4	0.312	0.307	0.019	0	0.010	0.018	0.017	0.011	0.093	0.012
<i>S. s. mosquensis</i>	5	0.316	0.313	0.002	0.017	0	0.001	0.011	0.038	0.100	0.011
<i>S. s. ciscaucasicus</i>	6	0.324	0.323	0.005	0.021	0.002	0	0.023	0.031	0.111	0.012
<i>S. s. uralensis</i>	7	0.327	0.327	0.012	0.029	0.008	0.008	0	0.041	0.112	0.023
<i>S. s. kastschenkoi</i>	8	0.319	0.309	0.029	0.017	0.029	0.029	0.041	0	0.101	0.022

Genetic differentiation

Eleven loci displayed fixation of alternative alleles (Idh-1, Ldh-B, Mod-1, Sod-1, Es-1, Es-2, Es-3, Es-10, Es-a, Hb-B, Tf) among part of the populations. From the allele frequencies at 36 loci studied, Nei's genetic distance (D) was calculated between taxa (Tab. 4). An UPGMA dendrogram summarizing the genetic relationships between the taxa investigated is given in figure 2.

There are two main clusters present in the phenogram. One of them consists of the nominative *S. s. sylvaticus* and includes *S. s. vohlynensis* also, the second cluster combines *S. microps* with all other taxa. The mean of standard Nei's genetic distance (Nei 1975) between "sylvaticus"-like and "microps"-like taxa is $D = 0.313$, which corresponds to a level of interspecies differentiation. The genetic distance between *S. s. vohlynensis* – *S. s. sylvaticus* was very low ($D = 0.004$). The mean genetic distance among "microps"-like group was higher, $D = 0.041$ ranging from 0.002 to 0.124. A valuable level of genetic differentiation among "microps"-like taxa appeared with the *S. s. pallipes*. Its mean genetic distance from the other "microps"-like taxa was $D = 0.113$, which corresponds to genetic differentiation of allopatric species.

The levels of genetic differentiation supported fixation of alternative alleles. Both *S. s. sylvaticus* and *S. s. vohlynensis* differed from the other taxa by the following alleles:

Es-1¹⁰⁰, Es-2¹¹⁰, Es-3¹⁰⁰, Es-10⁹⁹, Es-a¹⁰⁰, Hb-B¹⁰⁰, Ldh-B⁹⁸, Mod-1¹⁰⁵, Sod-1¹⁰⁵. The taxa identified as the “*microps*”-like displayed an alternative gene pool. The wood mouse from the Pamiro-Alay mountains, *S. s. pallipes*, can be characterized by fixation of some unique alleles (Es-1^{93,96}, Es-2^{99,102}, Tf^{97.5,99.5}, Idh-1^{95.5}), subspecies differing from other representatives of the “*microps*”-like species group.

Discussion

The analysis of genetic divergence among *S. sylvaticus* subspecies showed two main taxa groups at a species level of differentiation. One of them consists of the nominative *S. s. sylvaticus* (L.) and the *S. s. vohlynensis* at a very low level of divergence. Gene pools of these taxa are characterized by three alleles unique for the *Sylvaemus* genera, Sod-1¹⁰⁵, Mod-1¹⁰⁵, and Ldh-B⁹⁸ having an identification significance for *S. sylvaticus* (L.) in Europe (ENGEL et al. 1973; BENMEHDI et al. 1980; CSAIKL et al. 1980; CSAIKL 1983; GEMMEKE 1980, 1983; NASCETTI and FILIPPUCCI 1984; GEBZYNSKY et al. 1986; BRITTON-DAVIDIAN et al. 1991; FILIPPUCCI 1993; HARTL et al. 1992).

Comparison of data from the literature concerning *S. microps* diagnostic loci (CSAIKL et al. 1980; CSAIKL 1983; GEMMEKE 1983; FILIPPUCCI 1993; HARTL et al. 1992) and pairwise comparison of gene pool in *S. sylvaticus* – *S. microps* do not contradict one another in principle. According to data in the literature (CSAIKL et al. 1980; CSAIKL 1983; GEMMEKE 1983; FILIPPUCCI 1993), *S. microps* does not have unique alleles that can identify this species from the other representatives of wood mice genera. Only on the basis of diagnostic loci in pairwise comparisons can real diagnostics be achieved for *S. microps*. According to the presented data, all the “*microps*”-like taxa are characterized by two well-defined identification loci with fixations of Hb-B¹¹⁵ and Es-a^{100.5} alleles. From the methodical point of view, these suitable loci were not studied by previous investigators (CSAIKL et al. 1980; GEMMEKE 1983; FILIPPUCCI 1993).

The second group of taxa, including also nominative *S. microps*, is characterized by relatively high levels of genetic differentiation even at significant levels for interspecies comparisons. Therefore, Pamiro-Alay *S. s. pallipes* can be divided from the other investigated subspecies identified as *S. microps*.

Specimens of the Pamiro-Alay taxon *S. s. pallipes* can be identified on the basis of some unique allelic variants of investigated loci: Es-1^{93,94}, Es-2^{99,102}, Idh-1^{95.5}, Tf^{97.5,99.5}. Thus, results presented here on genetic differentiation support taxonomic distinctness of *S. s. pallipes* at the allospecies level. Special interest, in addition to the Pamiro-Alay wood mice taxa, should be given to the most oriental wood mouse form, *S. s. kastschenkoi*, dwelling in the Altai. Earlier it was found (MEZHHERIN and MICHAILENKO 1991) that specimens of this subspecies are characterized by two diagnostic loci coding nonspecific esterases, and which have been excluded from sample of loci in this publication. This fact confirms a small but significant level of genetic distinctness of *S. s. kastschenkoi*.

The present results, confirming species identity of oriental wood mouse subspecies with *S. microps*, are not surprising if we refer to some earlier publications devoted to the systematics of *S. sylvaticus* in its oriental range. Firstly, KRATOCHVIL and ROSICKY (1952) in their descriptions of *S. microps* assumed that wood mice of Tataria (*S. s. mosquensis*), the southeastern Russia (*S. s. ciscaucasicus*), and Turkestan (*S. s. microtis*) are identical to this species. ZIMMERMANN (1962) also presented data supposing that the traditional range of *S. sylvaticus* would be included in the range of *S. microps*. Crossings during 6 generations performed by STEINER (1979) have confirmed the presence of *S. microps* in northeastern Turkey. Moreover, on the basis of some morphological features he hypothesized that this species occurs in the Transcaucasus region and the mountainous areas of the Crimea.

An analysis of variation of morphological characters and some genetic features of occidental *S. sylvaticus* subspecies from the European part of the former USSR has found

that the subspecies, *S. s. uralensis* Pallas, 1811, is the oldest available name for a group of *S. microps*-like forms (VORONTZOV et al. 1992). Further investigations of the southern Ural (type locality "uralensis") including data about central Asian taxa (MEZHHERIN 1996) may confirm this point of view.

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Zusammenfassung

*Biochemische Systematik der Waldmaus *Sylvaemus sylvaticus* (L., 1758) sensu lato (Rodentia, Muridae) aus Osteuropa und Asien*

Mittels der elektrophoretischen Untersuchung von 36 Allozymloci wurde die taxonomische Zugehörigkeit der östlichen Unterarten von *Sylvaemus sylvaticus* überprüft. Fast alle östlichen Unterarten von *S. sylvaticus* (*charkovensis*, *baessleri*, *mosquensis*, *ciscaucasicus*, *uralensis*, *tsherga*, *pallipes*) wurden als der Spezies *Sylvaemus microps* s.l. zugehörig identifiziert. Lediglich *S. s. vohlynensis* ist nach wie vor der Art *S. sylvaticus* zuzuordnen. Die am weitesten im Osten vorkommenden Waldmäuse, *kastschenkoi* im Altaigebirge und *pallipes* in Tadjikistan, sind von der Nominatform *S. microps* durch mehrere fixierte allelische Unterschiede abzugrenzen. Derartige Unterschiede kennzeichnen sehr häufig verschiedene Arten. Die Subspezies *uralensis* Pallas, 1811 kann als ältestes valides Taxon innerhalb der Spezies *S. microps* gelten.

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